

Physical habitat and social conditions across a coral reef shape spatial patterns of intraspecific behavioral variation in a demersal fish

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Abstract

As coral reef ecosystems decline in health worldwide, reef-associated fishes are being impacted by changes to their coral reef habitats. While previous studies have shown coral reef structure to affect the demography of reef fishes, changes in reef conditions may also impact the behavior of reef fishes as they cope with altered habitats. In this study, we examined spatial patterns of intraspecific behavioral variation in the bicolor damselfish (*Stegastes partitus*) across the fringing reefs of Curaçao (Caribbean Sea), and explored how this behavioral variation associated with physical and social conditions on the reef. Principal components analysis (PCA) condensed physical parameters of the reef into principal component 1 (PC1), comprising depth, coral cover (%), rugosity, and average hole size (cm²), and principal component 2 (PC2), which represented the number of holes. PC1, but not PC2, increased spatially across the reef as the habitat transitioned from coral rubble in the shallows to live coral on the reef slope. This transition in reef structure was paralleled by changes in social conditions including decreases in bicolor damselfish density in habitats with higher PC1 values. The behavior of bicolor damselfish also varied spatially with greater aggression and more frequent shelter use in habitats with lower PC1 values. Path analysis revealed robust associations between this behavioral variation and physical habitat conditions of the reef, indicating that physical – rather than social – habitat variation is the primary determinant of these spatial patterns of intraspecific behavioral variation. Taken as a

whole, this coupling between physical reef structure and behavior suggests that reef fish may show altered behaviors on coral reefs degraded by anthropogenic impacts.

Introduction

Environmental variation holds a central role in determining the distribution and diversity of species. For any given taxon, the number and type of environmental variables that govern its distribution can range widely, but commonly include both abiotic parameters (e.g. temperature, salinity, wave energy, substratum shelter) and biotic variables such as food and social factors (e.g. conspecific density, local species diversity). Spatial heterogeneity in environmental conditions often equates to variation in habitat quality, which ultimately leads to variation in the distribution of species. However, less commonly considered is that environmental variation can also generate spatial variation in behavior within a species. Similar to other phenotypic traits, behavior can be strongly influenced by variation in habitat, and individuals that experience different physical and social conditions – whether along environmental gradients or among geographically isolated habitats – can differ behaviorally as they cope with disparate local challenges (Reichert 1974; Thompson 1990; reviewed by Foster 1999). Whether arising through evolutionary divergence (Magurran et al. 1995) or plastic changes in development (West et al. 2003; Ghilambor et al. 2010), such behavioral variation may have far-reaching consequences for the dynamics of populations and communities (Anholt 1997; Smith et al. 2000; Sutherland & Norris 2002). Understanding the ecological causes and significance of such habitat-associated intraspecific behavioral variation takes on a heightened importance as anthropogenic activities continue to change terrestrial and aquatic habitats globally.

Few ecosystems are seeing anthropogenic impacts more rapidly than the world's tropical coral reefs (Knowlton 2001; Pandolfi et al. 2003). Coral reef ecosystems are renowned for their extensive variation in physical and social conditions over small spatial scales (on the order of meters) and it is well established that the diversity and relative density of fishes supported by a

coral reef are linked to this structural complexity (e.g. Luckhurst & Luckhurst 1978; Roberts & Ormond 1987; Chabanet et al. 1997; Öhman & Rajasuriya 1998; Holbrook et al. 2002). Such habitat-associated patterns of fish abundance have been shown to be mediated in complex ways by spatial variation in the distribution of resources and the associated benefits and costs of obtaining those resources. For example, the distribution of Nassau grouper (*Epinephelus striatus*) at Great Exuma Island, Bahamas, was found to be mediated by body size-dependent tradeoffs between foraging and predation pressures (Dahlgren & Eggleston 2000). When juvenile grouper were small, they occupied macroalgal clumps where foraging opportunities were limited but predation risk was low; as fish grew to larger sizes, they moved to other structurally complex habitats with better foraging such as rock ledges and holes, live and dead coral, and sponges, as the risk of predation was now offset by the fish's larger body size (Dahlgren & Eggleston 2000). Behavioral mechanisms such as priority effects and competition also play roles in shaping the distribution of coral reef fishes, as behavioral interactions can force some individuals into less preferred habitats, leading to reduced reproductive success or lower survival (e.g. Munday 2001; Almany 2003, 2004). For instance, Bay et al. (2001) found that patterns of spatial distribution and habitat use for four species of *Dichistodus* damselfishes on the Great Barrier Reef, Australia, resulted from the combined effects of behavioral selection of particular habitats by juveniles and competitive exclusion of those juveniles by aggression from adult damselfish already established in those habitats. Similarly, in a study of two *Dascyllus* damselfish species, aggressive interactions in microhabitats with high densities of juvenile damselfish led to the redistribution of some juveniles to less preferred areas with greater predation risk (Holbrook & Schmitt 2002). Taken as a whole, these and other studies point to habitat characteristics and social factors interacting to influence the spatial distribution patterns and, ultimately, population and community dynamics of coral reef fishes (Anholt 1997; Smith et al. 2000; Sutherland & Norris 2002).

However, recent studies on the life history of coral reef fishes suggest that the physical and social characteristics of the local reef habitat can also interact to impact reef fishes in dimensions beyond presence–absence relationships. For instance, several studies have found that coral reef fishes can exhibit intraspecific variation in growth, body condition or demography that is linked to reef habitat characteristics (Pratchett et al. 2004; Kingsford & Hughes 2005; Afonso et al. 2008; Paddock et al. 2009). In one such study, Feary et al. (2009) found that two damselfish species, *Chrysiptera parasema* and *Dascyllus melanurus*, had reduced growth rates in disturbed reef habitats with more dead corals than in habitats with a high percentage of live coral cover, even though there were no differences in damselfish density between the habitats. Such habitat-associated variation in life history is likely to be mediated in part by intraspecific variation in behavior, given that behavior is also shaped by habitat characteristics. Although studies linking habitat characteristics, social factors, and intraspecific variation in behavior in coral reef fishes are sparse, one study that did look specifically for such relationships found that agonistic interactions among juvenile three-spot damselfish (*Stegastes planifrons*) were more frequent on small lagoonal patch reefs with a greater damselfish density than on continuous back reef habitats with a lower fish density (Levin et al. 2000). However, because fish densities and physical habitat conditions varied together, it was not possible to readily attribute the behavioral variation in these three-spot damselfish to only physical or social characteristics of the reef habitat (Levin et al. 2000). As illustrated by this study by Levin et al. (2000), determining the relative importance of specific physical and social parameters in driving patterns of intraspecific behavioral variation can be difficult methodologically. Many environmental factors influence behavior through a complex of interacting causes, and often several of these factors will co-vary in ecologically relevant contexts.

In this study, we explored how physical and social environmental conditions interact to shape patterns of intraspecific behavioral variation in the demersal bicolor damselfish (*Stegastes*

partitus). Among coral reef fishes, the bicolor damselfish is well suited as a model for investigating habitat effects on intraspecific behavioral variation given that this species is highly abundant on coral reefs throughout the Caribbean Sea and shows local habitat fidelity as it defends territories over the substratum (Booth & Hixon 1999). Previous studies have shown that the distribution of bicolor damselfish is related to the structural complexity and live coral cover of the local reef habitat (Nemeth 1997). However, the types of reef micro-habitats occupied by bicolor damselfish can vary widely, ranging from *Montastrea*-dominated reef to *Acropora* patches and even coral rubble (Nemeth 1998). Bicolor damselfish have also been shown to exhibit differences in juvenile growth and survival depending on the structure of their coral habitat (Nemeth 1998, 2005; Figueira et al. 2008), so that life history in this species appears to be influenced in some capacity by the biotic and/or abiotic conditions of the local habitat. More specifically, we quantified variation in physical characteristics (e.g. hole number, rugosity, coral cover) and social conditions (e.g. conspecific density, local fish species diversity) across the transition zone of a fringing reef from coral rubble to the reef slope, and then used path analysis to infer the direct and indirect influences of these physical and social parameters on spatial patterns of intraspecific behavioral variation in bicolor damselfish across this gradient of coral reef habitat conditions. Path analysis allows for the inferential testing of causal relationships among variables that interact in complex ways (Shipley 2000) and with this approach, we identified broad relationships between habitat characteristics and intraspecific behavioral variation in the bicolor damselfish and distinguished the relative strengths of several key physical and social habitat variables as causal influences on the expression of behavioral variation in these wild damselfish.

Study Area

Bicolor damselfish were studied at three fringing reef sites (Playa Kalki, Playa Jeremi, and Daaibooibaai) located along the southern, leeward side of Curaçao, the Netherlands Antilles

(Fig. 1), in the Southern Caribbean Sea from 16 to 31 May 2009. At each site, the coral reef varied spatially in structure from dead coral rubble located inshore to live coral cover (largely mixed *Montastrea* species) located near the reef crest and reef slope (Bruckner & Bruckner 2003).

Material and Methods

To assess how the behavior of bicolor damselfish varied relative to the physical and social characteristics of the reef habitat, we used SCUBA to establish 10 transect lines at each of the three sites. A starting point was haphazardly selected in the rubble habitat, and a single 30-m transect was placed parallel to the reef contour. Nine subsequent transects were then placed parallel to the initial transect, each 5 m further offshore than the previous one. This transect arrangement covered the variety of habitats at each site including the coral rubble, transitional zone, and live coral habitat. Along each transect, habitat characterization and damselfish behavior were recorded in eight 1-m² quadrats, resulting in a total of $n = 80$ quadrats per site, or $N = 240$ sampled quadrats for the three sites combined. Quadrat locations along the transect line were randomly allocated by using a random number generator to assign each quadrat's distance along the transect (minimum distance of 2 m between quadrats) as well as the placement of the quadrat on either the left or the right side of the transect line. Bicolor damselfish exhibit high site fidelity (Booth & Hixon 1999) and the spatial scales used in our survey design were chosen to ensure independence of fish observations based on preliminary studies by the authors; no bicolor damselfish were observed to move among quadrats or transects, and the alternating use of different fish size classes for behavioral observations (see description below) bolstered confidence that each replicate sample was independent. Within each quadrat, we characterized the behavior of a single bicolor damselfish and quantified several parameters that defined the immediate physical and social habitat.

[Insert Figure 1]

Fish behavior assessments

We observed the behavior of a single bicolor damselfish from each quadrat during 6-min focal observations on individual fish. All observations were conducted between 10:00 and 18:00 h. During each observation period, the frequency of aggressive chases and nips, shelter use, and courtship behavior (courtship dips) was recorded. These behaviors were selected to represent the main fitness-related behaviors commonly observed in this species during preliminary studies by the authors and were categorized according to descriptions provided in previously published ethograms of the species (Myrberg 1972). For aggressive behavioral exchanges, we also recorded which fish (focal or nonfocal) initiated the social interaction (as indicated in the categories 'by focal' or 'at focal', as well as the sum of these two categories of aggression or 'total aggression') and noted whether this interaction occurred between two bicolor damselfish or between the focal fish and another species. To avoid disturbing the behavior of damselfish, focal behavioral observations were conducted at each quadrat site prior to laying either the transect line or quadrat. Divers used the measuring lines on the transect tape to estimate accurately where the next quadrat would be placed, and observed a damselfish from 2 to 4 m away to avoid disturbing the behavior of the fish. At each quadrat location, the behavior of either one small (<4 cm, TL) or one large (>4 cm, TL) bicolor damselfish was observed. The demarcation between size classes was based on the size at which bicolor damselfish become sexually mature (e.g. Aguilar et al. 2008). It is well established that body size is a strong determinant of agonistic behavior in many fishes including the bicolor damselfish (Harrington 1993; Helfman & Winkelman 1997). Fish were therefore categorized into these two size classes so that behavioral observations encompassed the range of individual behavioral variation in the species and was not biased by sampling only a limited size class of damselfish. Selection of either a large or a small damselfish was predetermined for each quadrat in accordance with whether the quadrat was to be on the left or right side of the transect line. Individual fish fitting the predetermined size category were selected haphazardly within the

quadrat area by the observer, using markings on the transect tape and scale markings drawn on the quadrat itself to estimate fish size.

Assessment of social and physical habitats

Social environmental conditions were characterized within each quadrat after each behavioral observation. After the 1-m² quadrat was placed at the predetermined random position along a transect, observers waited 6 min before recording the density (calculated as no. fish m⁻²) and species designation of all fish within the quadrat area as instantaneously as possible.

Preliminary experiments that estimated fish numbers in the habitat area before and after quadrat placement found that 6 min was sufficient time for fish to resume normal activities, including returning to the area if the fish fled or retreated into shelter during placement of the quadrat.

The physical habitat within each quadrat was characterized by measuring the size and number of holes or crevices, rugosity, and percent (%) coral cover. Holes, defined as any crevice with greater depth than width that was also large enough for a bicolor damselfish to potentially use as shelter, were measured along two lines attached to the quadrat parallel to the direction of the transect. These two strings were placed at distances of 25 and 75 cm from the edge of the quadrat overlapping the transect line. Any holes located underneath these two strings were counted and measured. Hole size (cm²) was measured as the length of string spanning the hole opening and the width at the widest point of the hole perpendicular to the string (Nemeth 1998). Rugosity was measured with the 'chain and tape' method (Risk 1972; Luckhurst & Luckhurst 1978) (individual link length = 1.45 cm) at the 50-cm mark of the quadrat, running perpendicular to the transect line. All quadrats were photographed (Canon Powershot 990 IS camera; Canon USA Inc., Lake Success, NY, USA) and the percent coral cover was determined for each quadrat using CORAL POINT COUNT with EXCEL EXTENSIONS 3.6

(CPCe 3.6) (Kohler & Gill 2006), with a grid of 81 uniformly distributed points within each 1-m² quadrat.

Statistical analyses

As the purpose of this study was to examine patterns of behavioral variation in bicolor damselfish relative to variation in physical and social conditions, preliminary data analyses were conducted to examine homogeneity of coefficients of variation (Zar 1996) among the three sampling sites. An extended chi-square (Feltz & Miller 1996) revealed that coefficients of variation for three habitat variables and all behaviors were statistically similar among the three sampling sites; data from the three sampling sites were therefore pooled for subsequent analyses.

Principal components analysis (PCA) was performed to determine associations among these physical habitat variables. Because the physical habitat variables were measured on different scales, data for each variable were normalized by subtracting the mean and dividing by the standard deviation (McGarigal et al. 2000). This procedure transforms the variables into dimensionless and comparable units so that relationships among variables will not result from a difference in measurement scales. The number of principal components (PCs) retained was based on the eigenvalues; only those PCs with an eigenvalue greater than one (>1.0) were retained. The extracted PCs were then used as independent variables in subsequent analyses involving physical habitat variation.

Relationships between physical habitat and social conditions were examined in two ways: (i) by using quantile regression to examine relationships between the density of bicolor damselfish and physical habitat PCs and (ii) by least-squares regression to explore relationships between fish diversity and habitat PCs. Preliminary analyses where the number of bicolor damselfish in a quadrat was plotted against either physical habitat PC (PC1 or PC2, obtained above) revealed wedge-shaped distribution patterns. Such wedge-shaped patterns have been encountered previously in stock assessment studies (Terrell et al. 1996)

and indicate unequal variance for the response variable (bicolor damselfish density) along the range of the independent variable (either habitat PC). This unequal variance makes analysis by an ordinary least-squares regression inappropriate, given that such methods estimate a measure of central tendency, which may not be the best indicator of the overall pattern. Rather, the bounds of the distribution better represent the relationship; in such scenarios, quantile regression is suitable for assessing the upper and lower boundaries of a distribution (Scharf et al. 1998; Cade & Noon 2003). In this study, multiple quantiles (10th, 50th, and 90th) were calculated, and the slopes were analyzed for statistically significant differences from zero (STATA; StataCorp, TX, USA). Quantile regression analysis thus revealed whether an upper threshold existed in terms of the maximum number of bicolor damselfish present for any given value of a physical habitat PC.

Relationships between physical habitat PCs and social conditions were also assessed by calculating Shannon–Weiner diversity indices (H') for each of the 240 quadrats using PAST software (Hammer et al. 2001). Linear regression was then used to examine the relationship between H' and the habitat PCs. H' accounts for both the total number of species present and the number of individuals representing each species, so the index also provides information on evenness. An adjusted H' was also calculated after excluding bicolor damselfish from the dataset of species within each quadrat in order to allow for statistically independent assessment of how bicolor damselfish density related to overall fish diversity.

Damselfish behavior was analyzed first by comparing the frequencies of aggression (with aggressive chases and nips performed by the focal fish and received by the focal fish analyzed separately), shelter use, and courtship displays between large (>4 cm, TL) and small (<4 cm, TL) fish categories using t-tests. Because the behavior of large and small bicolor damselfish differed, subsequent analyses of behavior were calculated for each fish size separately. For large bicolor damselfish, ‘by focal’ and ‘total aggression’ were significantly correlated ($p = 0.931$; P

< 0.0001) (see Table 1); for that reason, we only discuss ‘by focal’ aggression for large fish as its statistical relationships are similar to ‘total aggression’. For small bicolor damselfish, ‘at focal’ and ‘total aggression’ were highly correlated ($p = 0.850$; $P < 0.0001$), so only ‘at focal’ aggression is discussed for the small bicolor damselfish.

[Insert Table1]

Path analysis models

Spearman rank correlations were used to examine whether bicolor damselfish behavior was related to physical (e.g. principal components) and social (e.g. H' and bicolor damselfish density) habitat parameters (Zar 1996). Given that statistically significant associations were found between the physical habitat PCs and social conditions, as well as between behavior and several of the physical and social conditions, we also performed path analyses to elucidate patterns of causal inference among variables (Shipley 2000). Path analysis models were constructed using AMOSTM 5.0 (Arbuckle 2003) with SPSS 16.0 (SPSS Inc., Chicago, IL, USA) to investigate which variables affected behavior directly or indirectly, and which pathways or relationships were strongest. This analysis is similar to multiple regression but allows the investigator to test a priori defined direct and indirect relationships; however, predictor variables can serve as both independent and dependent variables.

Given that the behavior of small and large bicolor damselfish differed, and that relationships of behavior to environmental parameters differed with fish size, path analysis using maximum likelihood estimation was performed separately for small and large fish. Multiple models were built for each damselfish size class using original variables from the physical habitat PCA, social conditions, and behaviors, and then each model was tested for goodness of fit. Because the use of strongly correlated predictor variables within a single path model can generate biased results, a single variable was chosen to represent habitat PC1, which originally contained four correlated habitat variables. After testing four different models, with each one containing a

different variable to represent habitat PC1, the model using 'depth' was selected as the best overall fit (Table 2). However, regardless of which variable was chosen to represent habitat PC1, the direction of PC1 influence on other parameters in the model was similar. All path analysis models used 'number of holes' to represent habitat PC2. The social conditions were used in the model as intermediate variables (serving as both predictors of behavior and responses to either physical conditions or behavior), and the final dependent variables in the models were the behavior variables. The final models for small and large bicolor damselfish also contained an adjusted fish diversity index (H') that did not consider bicolor damselfish in the dataset to ensure independence from another variable in the model: the density of bicolor damselfish. Using the same bootstrap approach as discussed below, the model with the adjusted H' measure was determined to be a better fit than the model containing unadjusted H' values.

For all models constructed, general goodness-of-fit measures were calculated with the following parameters: chi-square was the difference between the observed covariance from the expected, CFI (comparative fit index) provided an indication of the lack of fit accounted for by going from the null model to our defined model and should be close to 1, and RMSEA (root mean square error of approximation) allowed for comparison of non-nested models (should be <0.05). For each model determined to be of general good fit, a bootstrap approach with 1000 bootstrap samples with replacement was used to choose the single best-fitting model for each fish size (Linhart & Zucchini 1986). The model with the smallest average discrepancy between the implied moments obtained from the bootstrap samples and those of the overall sample (ML discrepancy) was determined to be the overall best-fit model.

[Insert Table 2]

Results

Relationships among physical and social habitat conditions

Principal components analysis reduced the five measured physical habitat variables [hole number, average hole size (cm^2), rugosity, % live coral cover, and depth] down to two independent PC axes, which together accounted for 66.34% of the variation observed in physical habitat conditions. Physical habitat PC1 (eigenvalue = 2.296) explained 45.92% of the variation in physical habitat, whereas habitat PC2 (eigenvalue = 1.021) explained an additional 20.14%. Rugosity, average hole size (cm^2), % coral cover, and depth all clustered along the PC1 axis, with each of these variables having positive loadings on PC1 (Table 3, Fig. 2). The positive loadings of each variable indicate that these environmental parameters varied together positively, so that as depth increased, increases were also seen in rugosity, % coral cover and average hole size. Habitat PC2, in contrast, only represented the number of holes, which also loaded positively (Table 3, Fig. 2). The bifurcation of the number of holes and average hole size into separate PCs indicates that these two physical habitat parameters varied independently across the range of coral reef habitats sampled.

[Insert Table 3]

[Insert Figure 2]

Social environmental conditions showed significant relationships with variation in the physical coral reef habitat. When the total density of bicolor damselfish was analyzed against PC1, a significantly negative slope was found at the 90th quantile ($t = -2.597$; $df = 239$; $P = 0.00998$) and the 50th quantile or median ($t = -3.614$; $df = 239$; $P = 0.0003$) but not at the lower bound (10th quantile), which had a slope of zero (Fig. 3A). The relationship between PC1 and the density of small damselfish showed a similar pattern with significantly negative slopes at the 90th ($t = -2.780$; $df = 239$; $P = 0.006$) and 50th quantiles ($t = -5.015$; $df = 239$; $P = 0.0001$), but a slope of

zero at the 10th quantile (Fig. 3B). However, the density of large damselfish showed a different pattern relative to PC1. Slopes of the relationships between large damselfish density and PC1 were not significant at the 10th ($t = 0.000$; $df = 239$; $P = 1.000$), 50th ($t = 0.000$; $df = 239$; $P = 1.000$) or 90th quantiles ($t = -1.910$; $df = 239$; $P = 0.057$) (Fig. 3C), indicating that the density of large bicolor damselfish did not vary significantly with changes in the PC1 dimension of physical habitat. Rather, the change in overall bicolor damselfish density with PC1 was caused by a decreased abundance of small bicolor damsel-fish with higher PC1 values. The diversity of fish species (H') also increased as physical habitat PC1 increased across the reef ($r^2 = 0.19$; $P < 0.0001$) (Fig. 4A). This relationship still holds if the H' values of zero are removed from the analysis ($r^2 = 0.21$; $P < 0.0001$).

The density of bicolor damselfish also showed associations with habitat PC2, with the total density of bicolor damselfish increasing with higher PC2 values at the 90th ($t = 4.131$; $df = 239$; $P = 0.0001$) and 50th quantile ($t = 2.315$; $df = 239$; $P = 0.021$) but not at the 10th quantile (Fig. 5A). The density of small damselfish increased with PC2 when examined at the 90th quantile ($t = 3.391$; $df = 239$; $P = 0.001$) and 50th quantile ($t = 2.888$; $df = 239$; $P = 0.004$), but again not at the 10th quantile (Fig. 5B). Large bicolor damselfish showed increasing densities with greater values of habitat PC2 at the 90th quantile ($t = 3.902$; $df = 239$; $P = 0.0001$) but no significant relationships at the 50th ($t = 0.000$; $df = 239$; $P = 1.000$) or 10th quantiles (Fig. 5C). Unlike with PC1, there was no significant relationship between fish diversity (H') and habitat PC2 ($r^2 = 0.0003$; $P = 0.802$) (Fig. 4B). This relationship is consistent even when the H' values of zero are excluded from the dataset ($r^2 = 0.0011$; $P = 0.632$).

Variation in bicolor damselfish behavior

The frequency of all three behaviors observed (aggression, shelter use, and courtship displays) differed between large and small damselfish (Fig. 6). Large bicolor damselfish exhibited higher

rates of 'by focal' aggression ($t = -5.685$; $df = 238$; $P < 0.0001$), chasing opponents nearly four times more often than did small fish. However, large bicolor damselfish received less aggression ('at focal') than small fish ($t = 4.413$; $df = 238$; $P < 0.0001$). Large bicolor damselfish were involved in more aggressive interactions overall ('by focal' and 'at focal' aggression frequencies combined) than were small damselfish ($t = -3.050$; $df = 238$; $P = 0.0025$). Large bicolor damselfish also entered shelters more often than small fish ($t = -2.246$; $df = 238$; $P = 0.0256$) and showed significantly elevated frequencies of courtship ($t = -3.679$; $df = 239$; $P = 0.0003$); only one of the 118 small bicolor damselfish was observed courting.

[Insert Figure 3 and 4]

Relationships between intraspecific variation in behavior and habitat

Significant relationships were also found between intraspecific variation in bicolor damselfish behavior and variation in physical habitat conditions. The frequencies of aggression, shelter use (Fig. 7) and courtship by large bicolor damselfish each showed significant negative relationships with increasing values of habitat PC1. Similarly, aggression and shelter use by small bicolor damselfish were also negatively associated with PC1 (Fig. 7). In contrast, behavior of large damselfish was not correlated with PC2. However, all measures of aggression by small bicolor damselfish (e.g. 'at focal', 'by focal', and total) were correlated negatively with habitat PC2, indicating that intraspecific variation in the behavior of small damselfish was associated with the number of holes in the local habitat area.

[Insert Figure 5]

Variation in bicolor damselfish behavior was also associated with variation in the social conditions of the local habitat. Aggression and shelter use by both large and small bicolor damselfish (and courtship dips for large fish) were negatively correlated with fish diversity (Table 1). For large bicolor damselfish, 'by focal' aggression was positively correlated with small and total bicolor damselfish densities, but not large bicolor damselfish density. For small

bicolor damselfish, 'at focal' aggression was not significantly correlated with the density of bicolor damselfish (Table 1). Large bicolor damselfish showed statistically significant positive correlations between 'by focal' aggression and both shelter use and courtship displays, even though no similar relationships were seen among the behaviors of small bicolor damselfish (Table 1).

Path analyses of behavior and habitat

Path diagrams and accompanying standardized path coefficients for the two best-fit path analysis models examining the relative influences of physical and social habitat conditions on intraspecific behavioral variation are shown in Fig. 8. The path model for large bicolor damselfish behavior explained 34% of the variation seen in 'by focal' aggression, 34% of the variation in shelter use, and 13% of the variation in courtship behaviors (Fig. 8A). Direct effects outweighed indirect effects in all cases except for the association between the proxy for PC1 ('depth') and courtship displays. The strongest relationship occurred between depth and 'by focal' aggression, where the negative path coefficient indicated a decrease in aggression with increasing habitat depth. A strong relationship was also present between depth and shelter use, where again the negative coefficient indicated a negative association between these variables. Total bicolor damselfish density showed a negative relationship with depth but a positive relationship with the number of holes (representative of habitat PC2) in the habitat. These results support our finding that bicolor damselfish density decreased with depth but increased with the number of holes in the benthos. A strong relationship was also found between 'by focal' aggression and shelter use, where the positive coefficient indicated that large damselfish that were more aggressive also tended to use shelter more frequently. The frequency of courtship displays was positively associated with both the total density of bicolor damselfish and the frequency of 'by focal' aggression in a given quadrat.

[Insert Figure 6]

The best-fit path analysis model for small damselfish behavior explained 23 and 27% of the variation in small bicolor damselfish shelter use and ‘at focal’ aggression, respectively (Fig. 8B). Similar to the model with large damselfish behavior, the physical habitat variables were directly associated with behavioral and social environmental variation, but neither of the social environmental variables had significant direct effects on behavior. As with large damselfish, the strongest relationships in the path model for small damselfish behavior were between depth and the two behavioral variables: shelter use and ‘at focal’ aggression. Negative path coefficients between depth and these two behaviors indicate that as depth increased, the frequency of ‘at focal’ aggression and shelter use by small bicolor damselfish decreased. The number of holes (PC2) was found to be positively associated with the total density of bicolor damselfish and a weak negative relationship was also found between the number of holes and ‘at focal’ aggression by small damselfish. The two social variables, fish diversity and bicolor damselfish density, were positively associated with each other, whereas the two behavior variables of aggression and shelter use were negatively associated. Similar to the model for the behavior of large bicolor damselfish, the best-fit model for small bicolor damselfish suggests physical characteristics, and not social characteristics, of the local habitat have the strongest role in predicting variation in the behavior of small bicolor damselfish.

Discussion

Coral reefs are one of the most structurally heterogeneous ecosystems in the ocean and have long served to exemplify how complex habitats can support high biological diversity, typically in the form of species diversity. Less commonly considered, however, is that the heterogeneity of coral reef environments may also play a role in facilitating intraspecific behavioral diversity, which may ultimately have consequences for individual reproduction (e.g. McCormick 2009) and survival (e.g. Holbrook & Schmitt 2002), as well as on fish distributions (e.g. Harrington 1993; Almany 2003, 2004) and even species coexistence and

community diversity (Lichstein et al. 2007; Yamauchi & Miki 2009). In this study, we provide evidence that the spatial variability of coral reef habitats can generate significant intraspecific diversity in reef fish behavior. Bicolor damselfish were found to vary behaviorally over small spatial distances (meters) in patterns associated with variation in the physical and social environmental conditions of the coral reef habitat. The strongest relationships occurred between variation in the behavior of large (>4 cm) bicolor damselfish and habitat PC1 (a composite variable of physical habitat consisting of the % coral cover, rugosity, size of holes in the benthos, and depth) so that as PC1 values increased, the frequencies of aggression, shelter use, and courtship by large damselfish decreased. Aggression and shelter use behaviors by small bicolor damselfish were also less frequent in reef habitats characterized by higher PC1 values. We also found significant relationships between damselfish behavior and PC2 – the physical habitat dimension representing the number of holes in the local habitat. Unlike PC1, which varied with depth and therefore position along the reef slope, the spatial distribution of PC2 values across the reef was more arbitrary; that is, the number of holes in a quadrat did not show any statistically significant association with the depth, rugosity, % coral cover or average size of holes (habitat PC1). The overall density of bicolor damselfish also varied with the PC1 and PC2 variables of physical habitat conditions. The density of bicolor damselfish was significantly greater in the shallow coral rubble (low PC1 values) areas with less coral cover and a lower rugosity. However, this spatial variation in overall damselfish density across the reef profile (as related to PC1 values) was driven exclusively by the density of small bicolor damselfish (<4 cm, TL), and not large damselfish (>4 cm, TL).

[Insert Figure 7]

The higher bicolor damselfish density in low structurally complex habitat contrasts with previously described generalized relationships between fish distributions and coral habitat complexity. However, there are many potential ecological and behavioral mechanisms that

could interact to drive this distribution pattern. For example, as the density difference that we observed was driven by more small (juvenile) bicolor damselfish in low PC1 value habitat areas, it is possible that this pattern results from differential mortality and/or the specific habitat requirements of these smaller fish. Nemeth (1997, 1998) found that juvenile bicolor damselfish experienced greater mortality on *Montastrea annularis* boulder coral as opposed to *Porites* rubble. Small fish may therefore preferentially occupy the shallow rubble area because the size of shelter holes is smaller (indicated by lower PC1 value), and these shelters better restrict both larger damselfish competitors and any but the smallest predators (Hixon & Beets 1993). Bicolor damselfish have also been documented to undergo a diet shift as they age and grow, switching from benthic algae and prey to a more planktonic diet (Myrberg 1972). It is therefore possible that benthic algae are more abundant in the rubble habitats in part due to the high density of occupied damselfish territories, so a greater number of small fish can also be supported. It is also possible that the behavior of the damselfish themselves, especially where the fish occur at high densities, may be altering the substratum cover. Several species of damselfish in the Pacific Ocean have previously been shown to alter the algal turf composition within their territories either by selective foraging on benthic algae or by aggressive exclusion of grazers from their territories (Ceccarelli 2007) and it is possible that the high density of small bicolor damselfishes in low PC1 habitats may have similar impacts. Lastly, some damselfishes exhibit ontogenetic shifts in habitat preferences; Lirman (1994), for instance, found juvenile three-spot damselfish (*Stegastes planifrons*) had a preference for dead coral, whereas adults preferred live coral. When such ontogenetic variation in habitat preferences exists, it is likely to have evolved from tradeoffs in the risks and benefits of living in a particular habitat at different developmental stages (e.g. Dahlgren & Eggleston 2000).

[Insert Figure 8]

Whatever the ecological and behavioral bases for the distribution pattern that we observed may be, it is clear from our results that bicolor damselfish rely on shelter for protection of themselves and their eggs, and local habitats with greater hole availability are likely to provide more opportunities for nesting sites and predator avoidance. Further support for this conclusion comes from our finding that densities of both large and small damselfish were greater in habitats with more holes (higher PC2 values). In the case of both PC1 and PC2, habitat-density relationships were best explained using quantile regression analysis. The results of this analysis indicated that values of PC1 and PC2 best predicted the maximum number of bicolor damselfish – and not the average number – within that local habitat, which implies that other factors not accounted for in the regression models must interact with habitat PC dimensions to determine the actual number of damselfish in a given quadrat.

One key variable that might contribute to lower than predicted densities is the behavior of damselfish themselves. Highly aggressive and territorial bicolor damselfish likely exclude many smaller conspecifics from their local area (e.g. Harrington 1993, 1995; Almany 2003, 2004), and individual variation in the propensity toward agonistic behaviors may result in damselfish density patterns that cannot be explained by physical habitat conditions alone. Support for this idea can be found in our path analysis models, which revealed a weak association between the spatial variation of bicolor damselfish behavior and their density. Such density–behavior associations are often considered from the perspective of conspecific density influencing behavior (e.g. Knell 2009) but aggressive behaviors can reciprocally alter patterns of habitat use and abundance of both conspecifics and heterospecifics (Petren & Case 1996; Langkilde et al. 2005).

All the same, the physical characteristics of the coral reef habitat – specifically PC1 – were identified as the strongest drivers of intraspecific variation in bicolor damselfish behavior. This behavioral variation was observed over distances of only —35 m as the reef transitioned from

shallower areas of *Acropora cervicornis* rubble to the *Montastrea* sp.-dominated fringing reef slope. The shallow rubble habitats (low PC1 values) have resulted largely from the extensive loss of *A. cervicornis* and other branching coral species from white band disease outbreaks during the 1980s (Bries et al. 2004; Wapnick et al. 2004 and citations within). These mass losses from disease, combined with impacts of coral bleaching, coastal development, and hurricanes, have significantly reduced live coral cover in shallow regions of the fringing reefs of Curaçao and nearby islands since the 1970s (Bak & Nieuwland 1995; Bak et al. 2005). Thus, the spatial variation in behavior we observed may be the result of recent changes in the coral reef structure within our study area. Such a finding points to the possibility that the changes in coral reef habitat structure resulting from natural or anthropogenic impacts may have under-appreciated implications for the behavior of coral reef fishes.

Size-dependent variation in fish behavior

Although the results of the current study indicate several environmental parameters may be interacting to shape spatial patterns of fish behavior, we found that physical habitat structure had the strongest influence on intraspecific behavioral variation in the bicolor damselfish. Specifically, the strongest statistical correlations detected between behavioral variation and environmental conditions were observed between ‘by focal’ aggression by large damselfish and habitat PC1. In contrast, small damselfish showed the strongest relationship between habitat PC1 and shelter use. Together, these findings suggest that intraspecific behavioral variation among bicolor damselfish is not only tightly coupled with physical habitat conditions, but also varies with fish size. Bicolor damselfish become sexually mature at around 3.5 cm total length (Aguilar et al. 2008), and as damselfish were distinguished by being either larger or smaller than 4 cm, inherent differences in behavior were expected between the two size classes of fish. We observed clear size-dependant behavioral variation, with large fish exhibiting higher aggression, using substrate shelters more frequently, and courting more often, and small bicolor damselfish

receiving significantly more aggression than large fish. These agonistic interactions were generally directed from the large bicolor damselfish, an observation of both the present study and previous work by others (Harrington 1993, 1995).

Perhaps of greater consequence for understanding how large and small bicolor damselfish might be using habitats differently, we found that suites of correlated behaviors differed between the two size classes. Frequencies of 'by focal' aggression, courtship and shelter use were all positively correlated in large bicolor damselfish, whereas small bicolor damselfish only showed a significant positive relationship between 'at focal' aggression and shelter use. This size-related difference in the type of aggression associated with shelter use suggests that large and small bicolor damselfish may be using substrate holes for different functions. Overtly aggressive, high courting males in the large fish category that used substratum shelters more frequently were likely defending nesting holes. Male bicolor damselfish need to constantly maintain the nest and protect it from intruders and nest predators (Myrberg 1972), which would explain positive relationships between offensive 'by focal' aggression, courtship, and shelter use in these large male bicolor damselfish (Knapp & Kovach 1991). Previous studies found that male bicolor damsel-fish visit eggs in shelters one to two times per minute during peak spawning months (Myrberg 1972), which is slightly higher than our observation of large bicolor damselfish entering shelters an average of 0.8 times per minute (see Fig. 6B).

For small bicolor damselfish, the positive association between 'at focal' aggression and shelter use may be best interpreted as small bicolor damselfish using substrate shelters for individual protection from large damselfish or predators, as opposed to use as nesting sites. Adult bicolor damselfish routinely attack juveniles that enter their territories, seemingly because the small fish will soon compete for the same shelters (Harrington 1993). Small bicolor damselfish that stray too far from shelter are likely subject to frequent aggression from larger males or potential predation from other fishes (e.g. Nemeth 1998; Holbrook &

Schmitt 2002). However, it is also important to note that a higher rate of shelter use (as measured by the number of times that focal fish entered substrate shelters per time) does not necessarily equate to greater time spent within shelters. The average time spent within a substrate shelter was not recorded in the present study but that time may be similar across size classes or even greater in small fish, especially as small fish appear to be using shelters to avoid predators and the aggression of their larger conspecifics.

Conclusions

Here, we found that bicolor damselfish exhibit patterns of behavioral variation across a gradient of coral reef habitat structure. At present, the mechanisms underlying the habitat-behavior association patterns observed here remain unknown, but may include plastic developmental responses of behavior to local environmental conditions (West et al. 2003), differential habitat selection by genetically or developmentally distinct juveniles during settlement (Nemeth 2005), post-settlement selection against particular behavioral phenotypes via predation or competitive exclusion (Figueira et al. 2008), or a combination of these or other factors. Controlled laboratory studies have demonstrated that environmental variables ranging from temperature to water flow can generate differences in behavior (e.g. Lema 2006; Carfagnini et al. 2009), and intraspecific behavioral variation in bicolor damselfish likely results from complex interactions between several physical and social conditions.

Nevertheless, our findings – combined with other studies identifying links between variation in fish demography and coral reef habitat structure (Kingsford & Hughes 2005; Afonso et al. 2008; Paddock et al. 2009) – indicate that spatial heterogeneity in coral reef habitat structure can lead to intraspecific variation in behaviors critical to reproduction and survival.

Considering that coral reefs are undergoing major structural changes resulting from the combined impacts of coastal development, coral bleaching, pollution, and disease (e.g. Pandolfi et al. 2003), future studies examining how the behavior and demography of reef-obligate

species respond to variation in the physical and social habitat promise to provide new insights into how reef species are impacted by changes to the world's coral reefs.

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Fig. 1. Map of Curaçao (12°7'0" N, 68°56'0" W), the Netherlands Antilles, in the Southern Caribbean Sea, with the three sampling sites indicated. The depth ranges for the three sampling sites are as follows: Playa Kalki: 2.7–12.8 m; Playa Jeremi: 6.1–12.2 m; Daaibaaibooi: 3.6–13.4 m.

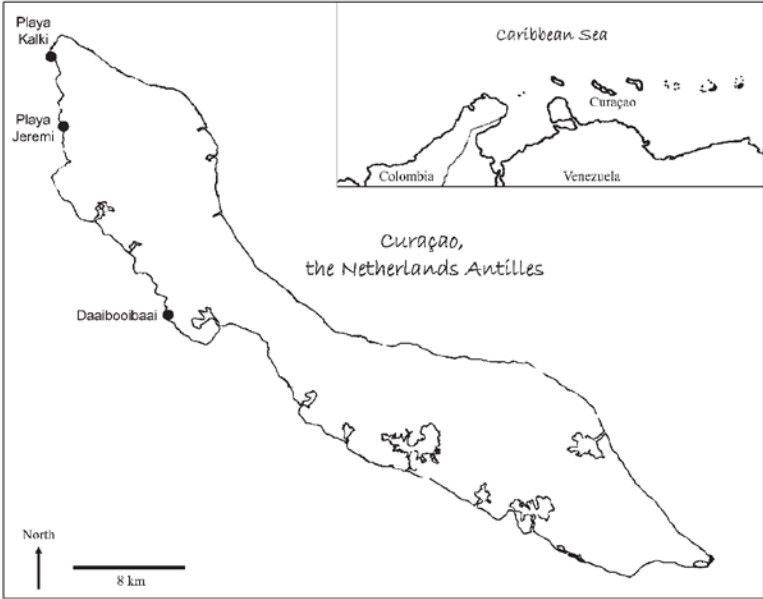


Table 1. Relationships betweenbicolor

damsel fish behaviors and			
Size	Correlated	Spearman's p	
Large	'Bv focal'	Shelter use	0.538
		Courtship	<0.0001
		Total BC	0.456
		Small BC	0.318
		Large BC	0.0004
Total fish	Bv focal	Shelter use	0.343
		Courtship	0.0001
		Shelter use	0.152
		Courtship	0.0928
Small	Shelter use	-	0.0006
		-	0.0003
		-	0.1026
		-	0.0181
		-	0.217
Total fish	'At focal'	Courtship	0.011
		Total BC	0.9026
		Small BC	-
		Large BC	0.3013
		Shelter use	0.117
All fish	Total BC	-	0.2057
		-	0.9025
		-	0.0038
		-	0.0235
BC, bicolor	Total fish	Courtship	-
		-	0.3059
		Total fish	0.334
			<0.0001

Table 2. Summary of model fit parameters for path analysis models of large and small bicolor

Habitat PC1 variable	χ^2	df	P	CFI	RMSEA	ML (mean t)
Small bicolor						
Average hole size	5.385	7	0.613	1.000	0.000	38.242 t
% Coral cover	11.517	8	0.174	0.944	0.061	41.630 t
Rugosity	6.695	8	0.570	1.000	0.000	38.668 t
Depth	8.831	8	0.357	0.992	0.030	35.087 t
Depth + adjusted	4.624	7	0.706	1.000	0.000	31.343 t
Large bicolor						
Average hole size	13.652	11	0.253	0.978	0.045	58.910 t
% Coral cover	17.377	12	0.136	0.959	0.061	57.405 t
Rugosity	12.333	11	0.339	0.989	0.032	52.741 t
Depth	11.338	10	0.332	0.992	0.033	51.236 t
Depth + adjusted	12.791	13	0.464	1.000	0.000	48.984 t

df, number of unspecified parameters; χ^2 , chi-square; CFI, mean square error of discrepancy (the average discrepancy between the implied moments obtained from the bootstrap

Table 3. Factor loadings for the principal

Variable	PC	PC2
Rugosity	0.5155	0.0279
Number of holes	-	0.9728
Average hole size (cm ²)	0.4963	-0.1514
% Coral cover	0.4939	0.1234
Depth	0.4902	0.1215

Bold loadings indicate the axis of strongest

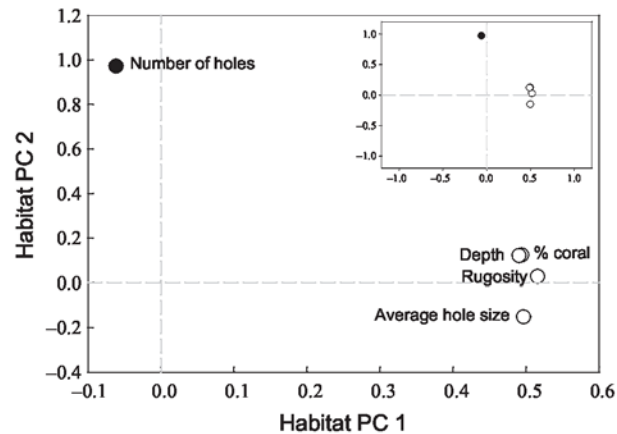


Fig. 2. Principal components analysis (PCA) for the five habitat variables. Original output is in the upper right corner. PCA reduced the five variables into two independent PCs.

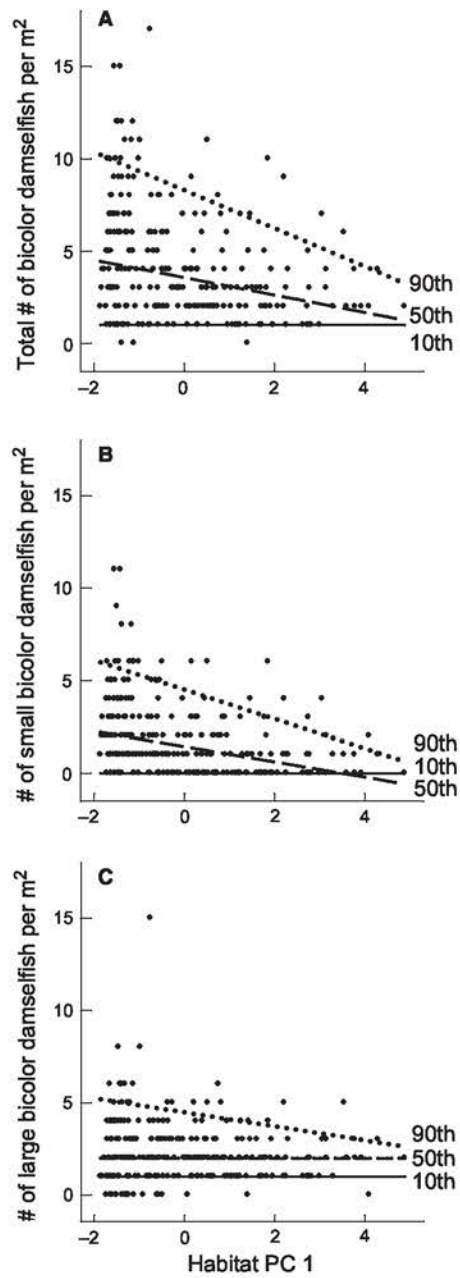


Fig. 3. Relationships of bicolor damselfish densities and physical habitat PC1 [comprising depth, coral cover (%), rugosity, and average hole size (cm²)] for (A) total bicolor damselfish density, (B) small fish only, and (C) large bicolor damselfish only. 90th, 50th, 10th are quartiles.

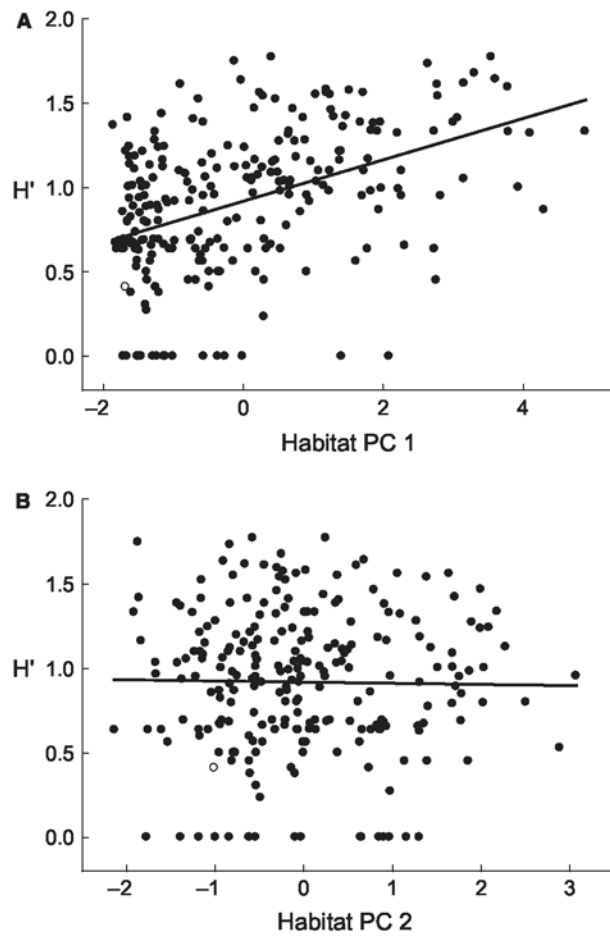


Fig. 4. Relationship between coral reef fish diversity (H') and (A) habitat PC1 and (B) habitat PC2. H' in this figure includes bicolor damselfish because H' is plotted against physical habitat parameters.

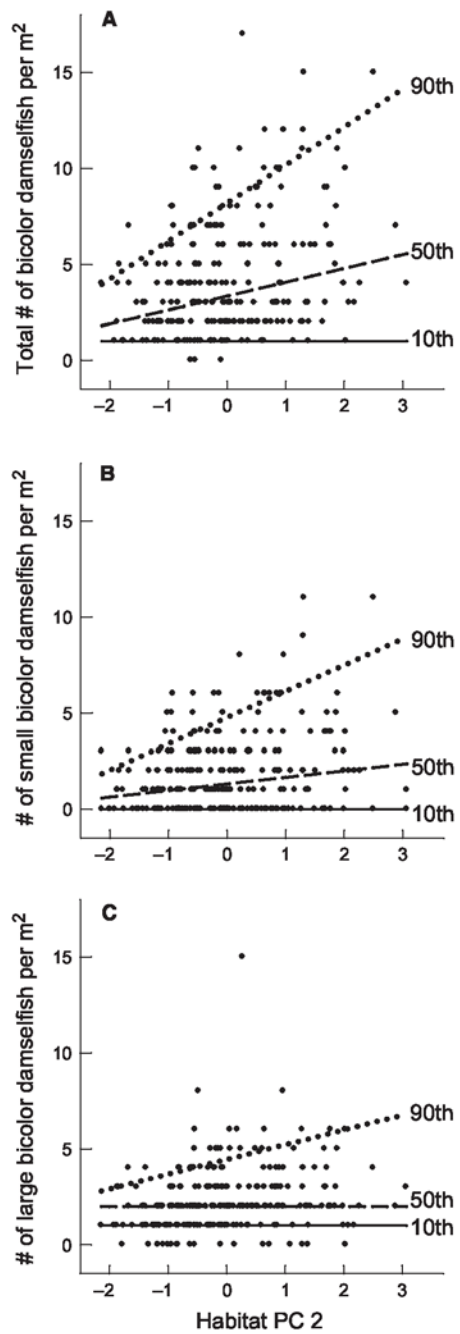


Fig. 5. Relationships of bicolor damselfish densities and physical habitat PC2 for (A) total bicolor damselfish density, (B) small fish only, and (C) large bicolor damselfish only. 90th, 50th, 10th are quantiles.

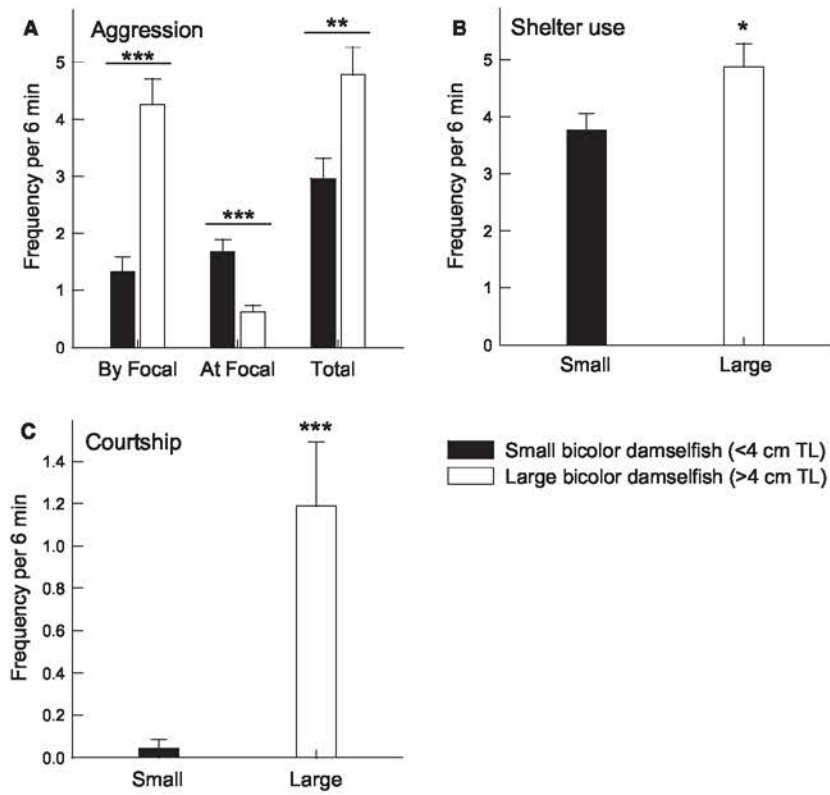


Fig. 6. Behavioral variation between large (>4 cm, TL) and small (<4 cm, TL) bicolor damselfish for (A) aggression, (B) shelter use, and (C) courtship dips. Asterisks indicate a statistically significant difference detected by t-tests between large and small bicolor damselfish (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

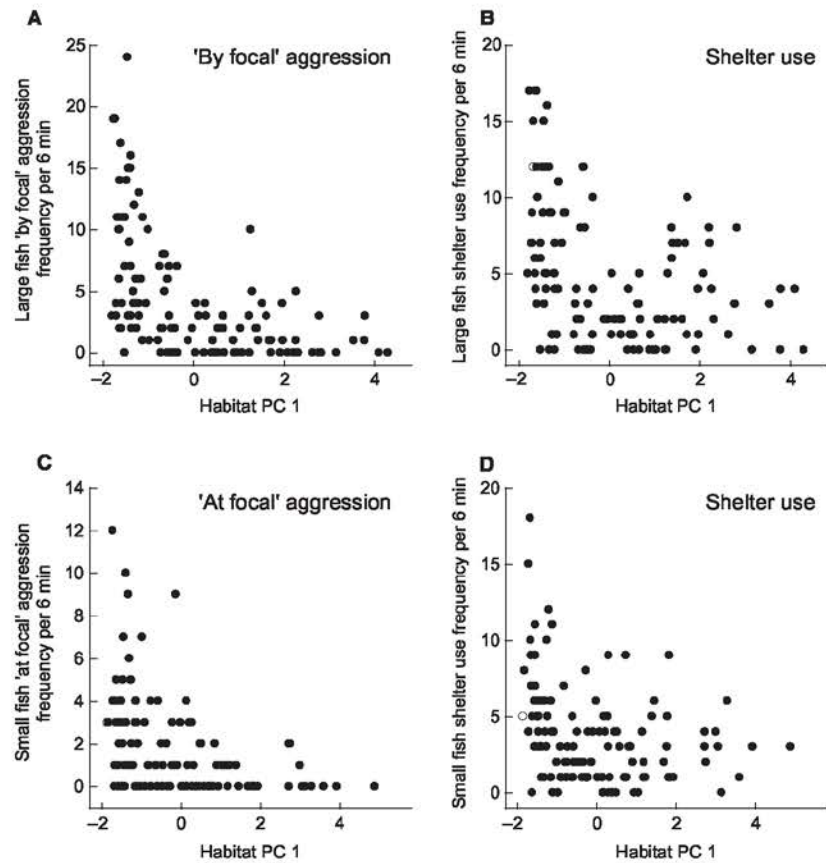


Fig. 7. Relationships between behavioral frequencies and physical habitat PC1 for large bicolor damselfish (A) 'by focal' aggression, (B) shelter use, and for small bicolor damselfish (C) 'at focal' aggression, and (D) shelter use.

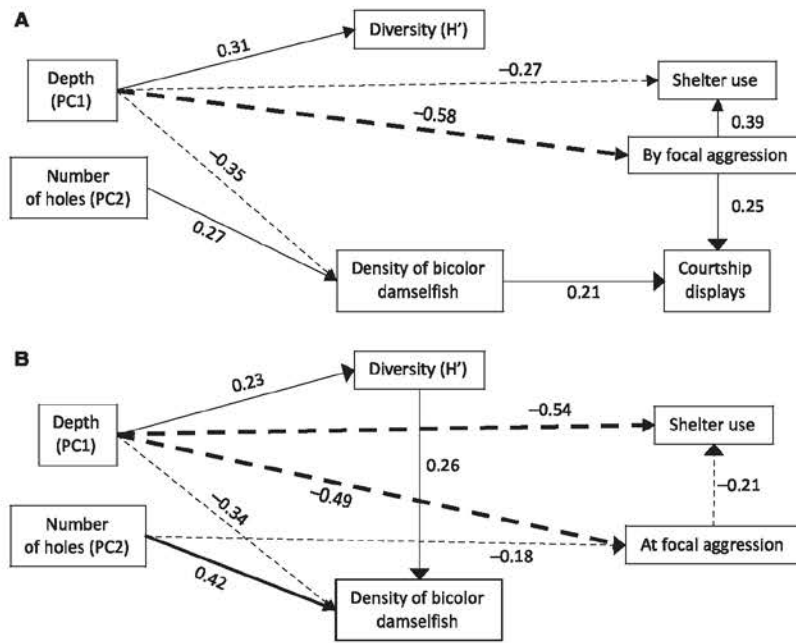


Fig. 8. Path analysis models for large (A) and small (B) bicolor damselfish. Depth is used as a proxy for habitat PC1 and the number of holes represents habitat PC2. Path coefficients are the standardized path coefficients, and the thickness of arrows is proportional to the strength. Dashed arrows indicate negative associations among the variables. All arrows are statistically significant in the model; non-significant arrows are not shown.